POLSKIE PISMO ENTOMOLOGICZNE
BULLETIN ENTOMOLOGIQUE DE POLOGNE
Tom 64: 261-277 Wrocław 30 XII 1995

**4TH SEMINAR ON APTERYGOTA, BIAŁOWIEŻA, POLAND, 1994**

# Phylogenetic study of the suborder *Arthropleona* (*Insecta*: *Collembola*) based on morphological characters and 18S rDNA sequence analysis

BYUNG-HOON LEE , UI-WOOK HWANG[2], WON KIM[2], KYUNG-HWA PARK[1], JIN-TAE KIM[1]

[1] Department of Biology Education, Jeonbug National University, Jeonju 560-756, Korea
[2] Department of Molecular Biology, Seoul National University, Seoul 151-742, Korea

ABSTRACT. Several hypotheses were proposed concerning the phylogeny of *Collembola*. They were all controversial due to the differences in character weighting as well as in methodology. In order to elucidate the phylogenetic relationship among groups of the suborder *Arthropleona* (*Collembola*), the morphological characters and the 18S rDNA nucleotide sequence data were analyzed in seven species of six families. Cladistic analysis was made with 28 morphological characters. Molecular phylogenies were also constructed by using the distance (neighbor-joining) and parsimony methods. The phylogenetic inference resulting from the morphological anaysis supports the traditional classification of *Arthropleona* in two superfamilies, *Poduroidea* and *Entomobryoidea*. The molecular results of the neighbor-joining method shows the limited congruence with the result produced by the morphological analysis. However, all the members of *Poduroidea* from a monophyletic lineage in both analyses. Within *Poduroidea*, the present study from morphological and molecular viewpoint indicates that the genus *Gulgastrura* should be excluded from the family *Hypogastruridae* as a separate lineage, allied with *Onychiurus* (*Onychiuridae*). The relationships of the families of *Entomobryoidea* proposed by early workers and the present morphological studies were not consistent with the present molecular data except, those processed with PAUP.

## INTRODUCTION

The classification and phylogenetic relationships among groups of the order *Collembola* have been a subject of disagreement among various authors (MAYNARD 1951, PACLT 1956, YOSII 1961, SALMON 1964, CASSAGNAU 1971, UCHIDA 1971, MASSOUD 1976). The situation is the same in the suborder *Arthropleona* within *Collembola*. Traditionally the suborder *Arthropleona* was classified in two superfamilies, *Poduroidea* and *Entomobryoidea* (BÖRNER 1901). However, several major questions concern the relatedness among families of each superfamily. In *Poduroidea*, some authors regarded the family *Onychiuridae* as more closely related with the family *Hypogastruridae* (YOSII 1961, SALMON 1964), whereas others considered the family *Neanuridae* closer to the family *Hypogastruridae* (PACLT 1956, CASSAGNAU 1971, UCHIDA 1971, MASSOUD 1976). Furthermore, it was suggested that *Neanuridae* and *Hypogastruridae* should be treated as two subfamilies of *Hypogastruridae* (CHRISTIANSEN, BELLINGER 1980). The systematic position of the genus *Gulgastrura* is also questionable, though traditionally this genus was included in *Hypogastruridae*. The morphological character reexamination of *Gulgastrura* as well as intermolting period investigation suggest a great divergence it should have undergone during its evolution from any existing *Collembola* groups (LEE, THIBAUD 1987).

In *Entomobryoidea*, there are also controversial views in the relatedness of *Tomoceridae* with other families. Some authors treated *Tomoceridae* as more closely related to *Entomobryidae* (PACLT 1956, CASSAGNAU 1971, MASSOUD 1976) while others considered *Tomoceridae* to be closer to *Isotomidae* (SALMON 1964, UCHIDA 1971). Another view assigned *Tomoceridae* as a subfamily of *Entomobryidae* (CHRISTIANSEN, BELLINGER 1980).

Under the controversial views on the classification and phylogeny of these apterygote insect, an attempt at applying a different method was made by one of the present authors who employed the cladistic analysis of morphological characters in subfamilial rank of *Neanuridae* (LEE 1985). Also molecular approaches such as isozyme or allozyme analysis were used by various authors to ascertain the intra- or inter-population, as well as inter-speciecific variation (DALLAI et al. 1983, FANCIULLI et al. 1985, 1986a,b, 1991, LEE et al. 1984, 1985, LEE, PARK, 1991). However, no efforts were aimed at testing any previous classification systems at the superfamily or family level of the suborder *Arthropleona*.

The arthropleonan phylogeny was examined in the present study by employing the cladistic analyses of morphological characters and 18S rDNA sequence data. The 18S rDNA sequence data are known as be effective in resolving the relationships among crustacean taxa at the infraorder level; such studies include that by one of the present authors (KIM and ABELE, 1990, SPEARS et al., 1992). In *Collembola*, the complete sequences of 18S rDNA of two species, *Hypogastrura dolsana* and *Crossodonthina koreana* were fully determined by a few of the present authors and the variability of the molecule was discussed (HWANG et al., in press). We present here the 18S rDNA sequence data for the inferences on the relationships among superfamilies and families of the arthropleonan *Collembola* insects.

## MATERIALS AND METHODS

Four species presumably representing each family of the superfamily *Poduroidea* and three species of families of the superfamily *Entomobryoidea* were collected from several localities of South Korea (Table 1). Specimens were either directly collected from soil and litter using brush or by extracting them with BERLESE funnels for 72 hours with lights on them.

Twenty eight morphological characters were selected for cladistic analysis and *Protura* were used as an outgroup to determine the character polarity among the groups of *Arthropleona* (Table 2). The data matrix of transformation series was prepared (Table 3) and analyzed using PAUP (Phylogenetic Analysis Using Parsimony) Version 3.0 program (SWOFFORD 1990).

In order to analyze the 18S rDNA nucleotide sequences of the seven arthropleonan species, published data were used for two species, and the complete sequences were determined for five species by means of PCR cloning and Taq sequencing. PCR-primer sites were located at both ends of the molecule (TACCTGGTTGATCCTGCC, TAATGATCCTTCCGCAGGTT). PCR-reaction was performed for 30 cycles (annealing 2', 52°C; extension 3', 72°C denaturation 1; 94°C). For blunt-ended ligation, the resulting fragments were modified using T4 Kinase and T4 Polynucleotide Polymerase by means of double Geneclean method (BIO 101). They were cloned in pUC 118. Sequencing was conducted by Taqtrac kit (Promega Co.) (KIM et al. 1992).

The sequence data were aligned by using the programs FASTA (PEARSON 1990) and Clustal V (HIGGINS et al. 1992). Molecular phylo-

Table 1
List of *Collembolan* species used in the present study; N = number of 18S rDNA nucleotides sequenced

| Classification | Species | N | Abbreviation |
|---|---|---|---|
| Phylum *Arthropoda* | | | |
| Class *Insecta* | | | |
| Order *Collembola* | | | |
| Suborder *Arthropleona* | | | |
| Superfamily *Poduroidea* | | | |
| Family *Hypogastruridae* | 1. *Hypogastrura dolsana* LEE and KIM, 1994 | 1,811 bp | Hd |
| (?) | 2. *Gulgastrura reticulosa* YOSII, 1966 | 1,810 bp | Gr |
| Family *Onychiuridae* | 3. *Onychiurus gangjinensis* LEE and KIM, 1994 | 1,805 bp | Og |
| Family *Neanuridae* | 4. *Crossodonthina koreana* YOSII and LEE, 1963 | 1,811 bp | Ck |
| Superfamily *Entomobryoidea* | | | |
| Family *Entomobryidae* | 5. *Homidia koreana* LEE and LEE, 1981 | 1,808 bp | Hk |
| Family *Isotomidae* | 6. *Isotoma choi* LEE, 1977 | 1,810 bp | Ic |
| Family *Tomoceridae* | 7. *Tomocerus kinoshitai* YOSII, 1954 | 1,810 bp | Tk |

Table 2
Transformation series of morphological characters. O, Plesiomorphy; 1-3, Apomorphies

| Character | Character states |
|---|---|
| 1. Body pigment | absent(0), coloured(1), with striking pattern(2) |
| 2. Integument | granulated(0), strongly tuberculated or smooth(1) |
| 3. Antennae | absent(0), present, 4 segm.(1), present, 4-6 segm.(2) |
| 4. Ant. III & IV | absent(0), subequal(1), ant.III > IV(2), commonly fused dorsally(3) |
| 5. Ant. annulate | w/o Ant.(0), absent(1), sometimes present(2), present(3) |
| 6. Apical organ | w/o Ant.(0), absent(1), present(2), |
| 7. III.A.O. | w/o Ant.(0), simple type(1), complex type(2), absent(3) |
| 8. P.A.O. | vesicle, one tubercle(0), oval shape, few vesicles(1), long, many vesicles(2), vesicles absent(3) |
| 9. Pseudocelli | present(0), absent(1) |
| 10. Eyes | present(0), absent(1) |
| 11. Mouthparts | chewing(0), modified for sucking(1) |
| 12. Spiracles on Th. III & IV | often present(0), absent(1) |
| 13. Th. I | visible(0),dorsally regressed but ventrally not(1), regressed(2) |
| 14. Setae on Th. I | present(0), absent(1) |
| 15. Body scale | absent(0), often present(1), present(2) |
| 16. Setae | simple(0),slightly differentiated(1), with many macrosetae(2) |
| 17. Bothriotrichia | absent(0), sometimes present(1), present(2) |
| 18. Troch. organ | absent(0), only in troch.(1), in troch. & femur(2) |
| 19. Claw | complete,simple(0), only Ung.(1), developed Ung. & Ungcl.(2) |
| 20. Abd.segm. | 12 segm.(0), 6 segm.(1) |
| 21. Anamorphosis | present(0), absent(1) |
| 22. Abd. III & IV | subequal(0), Abd. III < IV(1) |
| 23. Abd. I-III | with proleg(0), without prolegs(1) |
| 24. Ventral tube | absent(0), present(1) |
| 25. Tenaculum | absent(0),present, simple(1), developed(2) excessive reduction(3) |
| 26. Furcal complex | absent(0), normal(1), developed(2) excessive reduction(3) |
| 27. Dental spines | absent(0), often present(1), present(2) |
| 28. Anal spines | often present(0), present(1) |

genetic trees were constructed by two different tree making approaches, the distance (neighbor-joining) method using MEGA version 1.01 software (KUMAR et al. 1993) and the character-state (maximum parsimony) method using the PAUP program. Bootstrap method of data resampling (FELSENSTEIN 1985) was applied to evaluate the significance of the result.

## RESULTS AND DISCUSSIONS

The cladistic analysis of morphological characters yielded a single minimum-length tree with 56 steps (Fig. 1). The consistency index was 0.893. In this tree, *Arthropleona* were subdivided into two branches.

Table 3
Character data matrix of eight taxa of *Protura* and *Collembola*

| Taxa / character | *Protura* | *Gulgastrura reticulosa* | *Hypo-gastruridae* | *Onychiuridae* | *Neanuridae* | *Isotomidae* | *Entomo-bryidae* | *Tomo-ceridae* |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 1 |
| 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 3 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 |
| 4 | 0 | 1 | 1 | 1 | 3 | 1 | 1 | 2 |
| 5 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 3 |
| 6 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 |
| 7 | 0 | 3 | 1 | 2 | 1 | 1 | 1 | 3 |
| 8 | 0 | 3 | 1 | 2 | 1 | 0 | 3 | 3 |
| 9 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 |
| 10 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 11 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 12 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 13 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 2 |
| 14 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| 16 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 |
| 17 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 2 |
| 18 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| 19 | 0 | 0 | 0 | 0 | 1 | 2 | 2 | 2 |
| 20 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 21 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 22 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 23 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 24 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 25 | 0 | 3 | 1 | 3 | 3 | 1 | 2 | 2 |
| 26 | 0 | 3 | 1 | 3 | 3 | 1 | 2 | 2 |
| 27 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 |
| 28 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |

One of them, *Hypogastruridae*, branched first and *Neanuridae* next as a sister group of *Onychiuridae* and *Gulgastrura*. In the other branch, *Isotomidae* came off first and then *Tomoceridae* next with *Entomobryidae*.

Total length of 18S rDNA of the seven species ranges from 1805 to 1811, indicating that there is little length variation among the species (Table 1). The total aligned set of nucleotides of the seven species is shown in Appendix 1. The unrooted tree resulting from the neighbor-joining method using the data matrix of Table 4 shows that *Onychiuridae* cluster with *Gulgastrura*, and *Hypogastruridae* with the *Neanuridae* (Fig. 2). These four groups are clearly separated from the

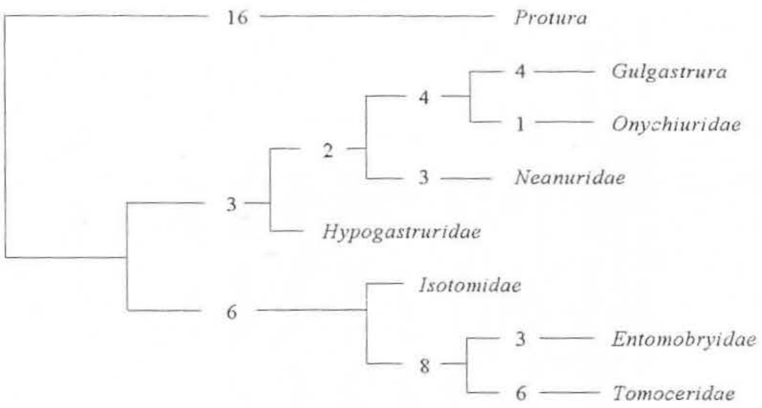


Fig. 1. Phylogenetic relationship of *Collembola* arthropleonan groups generated from maximum parsimony analysis based on morphological characters using PAUP. Numbers at nodes indicate the branch lengths at each node.

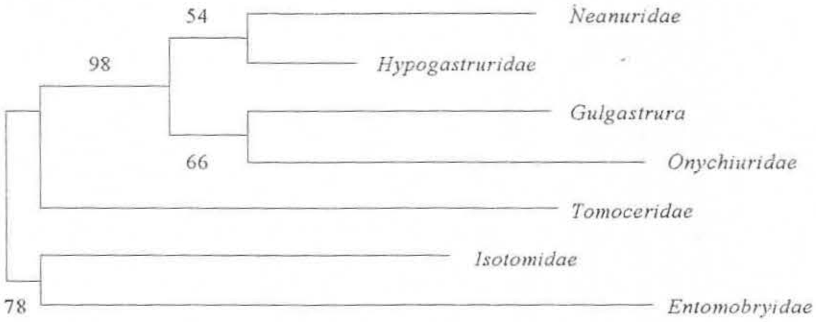


Fig. 2. Phylogenetic relationship of *Collembola* arthropleonan groups generated from neighbor-joining analysis of 18S rDNA sequence data. Numbers at nodes indicate the bootstrap percentages from 1000 samples.

remaining three groups as supported by the bootstrap value of 98%. Of three remaining groups, *Isotomidae* cluster with *Entomobryidae* rather than with *Tomoceridae*.

Maximum parsimony analysis yielded a single minimum-length tree of 306 steps with 78 informative sites (Fig. 3A). The consistency index was 0.788. The sequence alignment gaps were excluded from the analysis. In this tree, *Onychiuridae* clusters with *Gulgastrura*. *Isotomidae* combine with *Tomoceridae*, and these two groups have a

Table 4

Evolutionary distance data for 18S rDNA sequences of Collembolan species investigated. Upper right half gives JUKES and CANTOR (1969)-corrected estimates of sequence divergence calculated from the multiple aligned set of sequences with the compute distance program in MEGA version 1.01 (KUMAR et al., 1993) for use in a neighbor-joining analysis (SAITOU and NEI, 1987)

| | Hd | Gr | Og | Ck | Ic | Hk | Tk |
|---|---|---|---|---|---|---|---|
| *Hypogastruridae* (Hd) | — | 0.0330 | 0.0430 | 0.0330 | 0.0301 | 0.0519 | 0.0389 |
| ? (Gr) | | — | 0.0424 | 0.0477 | 0.0400 | 0.0621 | 0.0483 |
| *Onychiuridae* (Og) | | | — | 0.0471 | 0.0495 | 0.0688 | 0.0513 |
| *Neanuridae* (Ck) | | | | — | 0.0471 | 0.0669 | 0.0531 |
| *Isotomidae* (Ic) | | | | | — | 0.0430 | 0.0336 |
| *Entomobryidae* (Hk) | | | | | | — | 0.0573 |
| *Tomoceridae* (Tk) | | | | | | | — |

sister group relationship with *Entomobryidae*, and then with the *Hypogastruridae*. However, bootstrap analysis does not support the relationship of *Isotomidae* and *Tomoceridae* (Fig. 3B). It is noticeable, notwithstanding, that the three families, *Isotomidae*, *Entomobryidae* and *Tomoceridae*, combined together conforming to the classical monophyly of the superfamily *Entomobryoidea*.

The present results of the cladistic analysis of morphological characters agree with the traditional classification of *Arthropleona* in two superfamilies. However, the 18S rDNA sequence analysis yields only a limited support to this scheme. The neighbor-joining method supports clearly Poduroidean grouping but not the Entomobryoidean one (Fig. 2). The maximum parsimony method, however, does not support monophyly of the superfamily *Poduroidea* but suggests the single grouping of three families of *Entomobryoidea*. Considering

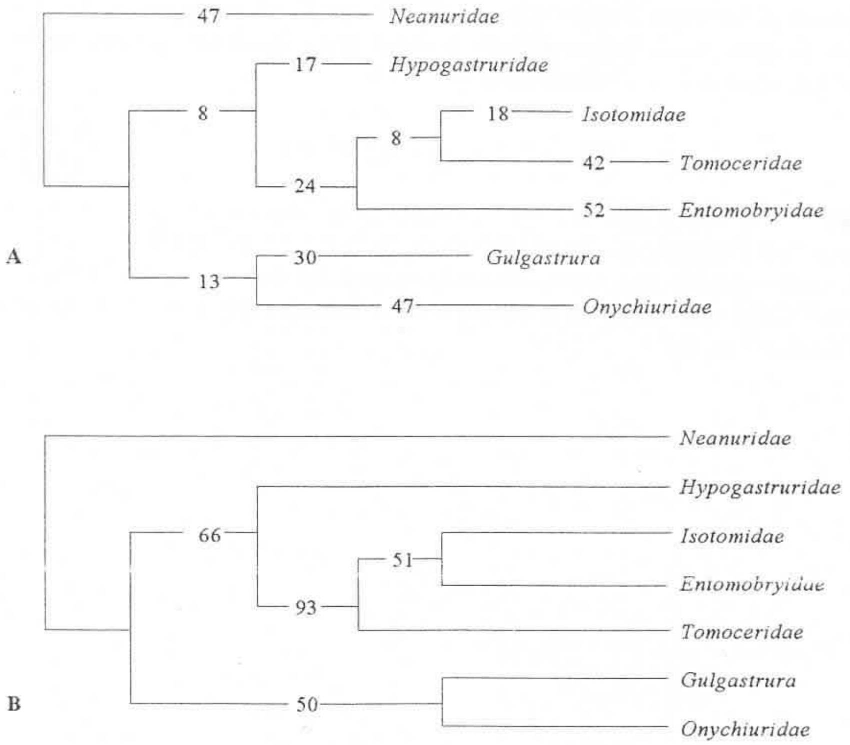


Fig. 3. Phylogenetic relationship of *Collembola* arthropleonan groups generated from maximum parsimony analysis based on 18S rDNA sequences using PAUP. A, Minimum-length phylogenetic tree. Numbers at nodes indicate the branch lengths at each node. B, Bootstrap 50% majority-rule consensus tree. Numbers at each node indicate the bootstrap percentages from 1000 samples.

the small number (78) of informative sites, the parsimony methods seem to be less applicable to such data than the neighbor-joining method.

The present study reveals that the cladistic analysis of morphological characters supports the classical taxa of *Poduroidea* and *Entomobryoidea* respectively. With molecular analysis, however, the superfamily *Poduroidea* is not supported except by Neighbor-Joining even though the separation of *Gulgastrura* from *Hypogastruridae* remains intact. For the superfamily *Entomobryoidea*, the grouping of the three families are supported only by maximum parsimony method. Close affinity of *Entomobryidae* to *Tomoceridae* resulting from the cladistic analysis of morhological characters supports the systems of PACLT (1956), CASSAGNAU (1971) and MASSOUD (1976). However the 18S rDNA sequence analyses give contradictory results when the two different methods are used. Therefore, the conventional view of the sister group relationship between *Tomoceridae* and *Entomobryidae* remains to be solved, though the present morphological data analysis agrees with the traditional view of these two families.

## ACKNOWLEDGEMENTS

This work was supported by the grant from the Korea Science and Engineering Foundation (KOSEF 91-0500-12-01-3) during 1991-1993. Additional support was made available partially by the Basic Science Research Institute Program, Ministry of Education, 1993. (Project No. BSRI-'93-414).

## Appendix 1.

Aligned sequence data of 18S rDNA from seven *Collembola* species. - indicates alignment gap. Ck - *Crossodonthina koreana*; Hd - *Hypogastrura dolsana*; Gr - *Gulgastrura reticulosa*; Og - *Onychiurus gangjinensis*; Ic - *Isotoma choi*; Hk - *Homidia koreana*; Tk - *Tomocerus kinoshitai*.

```
Ck  TCCCTGGTTGATCCTGCCAGTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTTCAAGCGAAAAATAA
Hd  TCCCTGGTTGATCCTGCCAGTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTTCAAGCGAAAA-TAA
Gr  TCCCTGGTTGATCCTGCCAGTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTTCAAGCAAAAA-TAA
Og  TCCCTGGTTGATCCTGCCAGTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTTCAAGCAAAAA-TAA
Ic  TCCCTGGTTGATCCTGCCAGTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTTCAAGCGAAAA-TAA
Hk  TCCCTGGTTGATCCTGCCAGTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTTCAAGCGAAAA-TAA
Tk  TCCCTGGTTGATCCTGCCAGTAGTCATATGCTTGTCTCAAAGATTAAGCCATGCATGTCTAAGTTCAAGCGAAAA-TAA

Ck  AGTGAAACCGCGAATGGCTCATTATATCAGTTATGGTTCCTTAGATCGTACTTACTACTTGGATAACTGTGGTAATTCT
Hd  AGTGAAACCGCGAATGGCTCATTATATCAGTTATGGTTCCTTAGATCGCACTTACTACTTGGATAACTGTGGTAATTCT
Gr  AGTGAAACCGCGAATGGCTCATTATATCAGTTATGGTTCCTTAGATCGCACTTACTACTTGGATAACTGTGGTAATTCT
Og  AGTGAAACCGCGAATGGCTCATTATATCAGTTATGGTTCATTAGATCGCACTTACTACTTGGATAACTGTGGTAATTCT
Ic  AGTGAAACCGCGAATGGCTCATTACATCAGTTATGGTTCCTTAGATCGCACTTACTACTTGGATAACTGTGGTAATTCT
Hk  AGTGAAACCGCGAATGGCTCATTACATCAGTTATGGTTCCTTAGATCGCACTTACTACCTGGATAACTGTGGTAATTCT
Tk  AGTGAA-CCGCGAATGTCTCATTAAATCAGTTATGGTTCCTTAGATCGCACTTACTACTTGGATAACTGTGGTAATTCT

Ck  AGAGCTAATACATGCGTTGGGCTCCAACTTTCG-GGAAGGAGCGCTTTTATTAGATCAAAGCCAATCGAACTCTCGGGTT
Hd  AGAGCTAATACATGCGTTGGGCTCCAACCCTCGTGGACGGAGCGCTTTTATTAGATCAAAGCAAATCGGACCTTCGGGTT
Gr  AGAGCTAATACATGCGCTGAGCTCCAACCCTCGTGGAAGGAGCGCTTTTATTAGATCAAAGCCAATCGGGCCTCCGGGTT
Og  AGAGCTAATACATGCGCTGGGCTCCAACCCTCTGGGAAGGAGCGCTTTTATTAGATCAAAGCCAATCGGACTTTCGGGTT
Ic  AGAGCTAATACATGCGCTGGGCCCCAACCCTCGTGGAAGGGGCGCTTTTATTAGATCAAAGCCAATCGGGCCTTCGGGTT
Hk  AGAGCTAATACATGCGCAGAGCCCCAACCCTCGTGGAAGGGGCGCTTTTATTAGATCAAAGCCAATCGGGTTTC—GGCT
Tk  AGAGCTAATACATGCGCTGGGCCCCAACCCTCGTGGAAGGGGCGCTTTTATTAGATCAAAGCCAATCAGTCTTTCGGGAC

Ck  CGTTTAATTGGTGACTCTGAATAACATTGCTGATCGCACGGTCTTGCACCGGCGACGTATCTTTCAAGTGTCTGCCTTAT
Hd  CGTTTTGTTGGTGACTCTGAATAACTTTGCTGATCGCACGGTCTCGTACCGGCGACGTATCTTTCAAGTGTCTGCCTTAT
Gr  CGTTTTGTTGGTGACTCTGAATAACTTTGCTGATCGCACGGTCTCGCACCGGCGACGTATCTTTCAAGTGTCTGCCTTAT
Og  CGTTTACTTGGTGACTCTGAATAACTTTGCTGATCGTACGGTCTCGCACCGACGACGTATCTTTCAAGTGTCTGCCTTAT
Ic  CGTTTAATTGGTGACTCTGAATAACTTTGCTGATCGCACGGTCTCGTACCGGCGACGTATCTTTCAAGTGTCTGCCTTAT
Hk  CGTTTTTTTGGTGACTCTGAATAACTTTGCTGATCGCATGGTCTCGTACCGGCGACGTATCTTTCAAGTGTCTGCCTTAT
Tk  TGTTATGTTGGTGACTCTGAATAACTTTGCTGATCGTATGGTCTTGTACCGACGACGTATCTTTCAAGTGTCTGCCTTAT
```

```
Ck  CAACTGTCGATGGTAGGTTATGCGCCTACCATGGTTGTAACGGGTAACGGGGAATCAGGGTTCGATTCCGGAGAGGGAGC
Hd  CAACTGTCGATGGTAGGTTATGCGCCTACCATGGTTGTAACGGGTAACGGGGAATCAGGGTTCGATTCCGGAGAGGGAGC
Gr  CAACTGTCGATGGTAGGTTATGCGCCTACCATGGTTGTAACGGGTAACGGGGAATCAGGGTTCGATTCCGGAGAACGGGT
Og  CAACTGTCGATGGTAGGTTATGCGCCTACCATGGTTGTAACGGGTAACGGGGAATCAGGGTTCGATTCCGGAGAGGGAGC
Ic  CAACTGTCGATGGTAGGTTATGCGCCTACCATGGCGGTAACGGGTAACGGGGAATCAGGGTTCGATTCCGGAGAGGGAGC
Hk  CAACTGTCGATGGTAAGTTATGCGCTTACCATGGTTGTAACGGGTAACGGGGAATTAGGGTTCGATTCCGGAGAGGGAGC
Tk  CAGCTGTCGATGGTAGGTTATGCGCCTACCATGGTTGTAACGGGTAACGGGGAATCAGGGTTCGATTCCGGAGAGGGAGC

Ck  CT-GAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCAGAACGGGGAGGTAGTGACGAA
Hd  CT-GAGAAACGACTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAA
Gr  CT-GAGAAACGGCCAGTACTCTTAAGAGAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAA
Og  TTCGAGAAATAGCTACCACCTCTAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAA
. Ic  CT-GAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCAGCTCGGGGAGGTAGTGACGAA
Hk  CT-GAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCAGCACGGGGAGGTAGTGACGAA
Tk  CT-GAGAAACGGCTACCACGTCCAAGGAAGGCAGCAGGCGCGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACGAA

Ck  AAATAACGATACGGAACTCATACGAGGCTCCGTAATCGGAATGAGTACACTTTAAATCCTTTAACAAGGATCCATTGGAG
Hd  AAATAACGATACGGAACTCATACGAGGCTCCGTAATCGGAATGAGTACACTTTAAATCCTTTAACGAGGATCTATTGGAG
Gr  AAATAACGATAGGGAACTCATACGAGGCTCCGTAATCGGAATGAGTACACTTTAAATCCTTTAACGAGGATCTATTGGAG
Og  AAATAACGATACGGAACTCATACGAGGCTCCGTAATCGGAATGAGTACACTTTAAATCCTTTAACGAGGATCTATTGGAG
Ic  AAATAACGATACGGAACTCTTACGAGGCTCCGTAATCGGAATGAGTACACTTTAAATCCTTTAACGAGGATCTATTGGAG
Hk  AAATAACGATGCTAAACTCATACGAGGCTTAGCAATCGGAATGAGTACACTTTAAATCCTTTAACGAGGATCTATTGGAG
Tk  AAATAACGATACGGAACTCATACGAGGCTCCGTAATCGGAATGAGTACACTTTAAATCCTTTAACGaGGATCTATTGGAG

Ck  GGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATCAGAATTGTTGTGGTTAAAAAGCTCGTAG
Hd  GGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGTGGTTAAAAAGCTCGTAG
Gr  GGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGCTGTGGTTAAAAAGCTCGTAG
Og  GGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGCTGTGGTTAAAAAGCTCGTAG
Ic  GGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAATGTTGTTGCGGTTAAAAAGCTCGTAG
Hk  GGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAATTTTGCTGTTGTTAAAAAGCTCGTAG
Tk  GGCAAGTCTGGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAG

Ck  TTGGATCTCGGTTTCAGGTGAATGGTGCATCTTGCGATGTTTTACTATTTGCTTGGACGATTTTGTTGGTTCGTTCATAG
Hd  TTGGATCTCGGTTTCAGATGGGCGGTGCACCTTGCGGTGTTT-ACTGTCTGTTTGGACGATTTTGTTGGTTCGTTCATGG
Gr  TTGGATCTCGGTTTCGGGTGAGCGGTGCACCTTGCGGTGTTT-ACTGTTTGCCCGGACGATTTTGTTGGTTCGTTTATGG
Og  TTGGATCTCGGTTTCGGATGATCGGTGC—TTGCGGTGTCT-ACTGGTTGTTCGGACGATTTTGTTGGTTCGTTTATAG
Ic  TTGGATCTCGGTTTCGGGCGAGCGGTGCACCTTGCGGTGTTT-ACTGCCTGCCCGGACGATTTTGTTGGTTCGTTTATGG
Hk  TTGGATCTCGGTTTCGGGCGGGTGGTGCGCCTTGCGGCGTTT-ACTGTCTGCCCGGACGATTATGTTGGTTCGTTCATGG
Tk  TTGGATCTCGGTTTCGGTTGGGTGGTGCACCTTGCGGTGTTT-ACTGTCTGACCGGACGATTTTGTTGGTTCGTGTATAG
```

```
Ck  GGGGGAGTATGGTTGCAAAGCTGAAACTTAAAAGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTT
Hd  GGGGGAGTATGGTTGCAAAGCTGAAACTTAAAAGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTT
Gr  GGGGGAGTATGGTTGCAAAGCTGAAACTTAAAAGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTT
Og  GGGGGAGTATGGTTGCAAAGCTGAAACTTAAAAGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTT
Ic  GGGGAAGTATGGTTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTT
Hk  GGGGAAGTATGGTTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTT
Tk  GGGGAAGTATGGTTGCAAAGCTGAAACTTAAAGGAATTGACCGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTT

Ck  GACTCAACACGGGAAATCTCACCAGGCCCGGACACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTCGGTGGGTG
Hd  GACTCAACACGGGAAATCTCACCAGGCCCGGACACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTCGGTGGGTG
Gr  GACTCAACACGGGAAATCTCACCAGGCCCGGACACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTCGGTGGGTG
Og  GACTCAACACGGGAAATCTCACCAGGCCCGGACACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTCGGTGGGTG
Ic  GACTCAACACGGGAAATCTCACCAGGCCCGGACACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTCGGTGGGTG
Hk  GACTCAACACGGGAAAACTCACCAGGCCCGGACACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTCGGTGGGTG
Tk  GACTCAACACGGGAAATCTCACCAGGCCCGGACACCGGAAGGATTGACAGATTGAGAGCTCTTTCTTGATTCGGTGGGTA

Ck  GTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCGATAACGAACGAGACTCTGGCCTATTAACT
Hd  GTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCGATAACGAACGAGACTCTGGCCTACTAACT
Gr  GTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCGATAACGAACGAGACTCTGGCCTACTAACT
Og  GTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCGATAACGAACGAGACTCTGGCCTACTAACT
Ic  GTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCGATAACGAACGAGACTCTGGCCTACTAACT
Hk  GTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCGATAACGAACGAGACTCTGGCCTACTAACT
Tk  GTGGTGCATGGCCGTTCTTAGTTGGTGGAGCGATTTGTCTGGTTAATTCCGATAACGAACGAGACTCTGGCCTACTAACT

Ck  AGACGTTATATCCTATTATGGGTTTGACGATGCTTCTTAGAGGGACGGGCGGCTTTTAGCCGCACGAGAATGAGCAATAA
Hd  AGACGTCAGATCC-TTTATGGGTCTGTCGTAGCTTCTTAGAGGGACGGGCGGCGTTTAGCCGCACGAGAATGAGCAATAA
Gr  AGACGACAGATTC-TTTA-GGGTTTGTCGTAGCTTCTTAGAGGGACGGGCGGCGTTTAGCCGCACGAGATTGAGCAATAA
Og  AGACAATGTATCC—TCG-GGGTTCATTGCTGCTTCTTAGAGGGACGGGCGGCTTTTAGCCGCACGAGAATGAGCAATAA
Ic  AGACGTTAGATCCCTTTGTGGGTCTATCGCAGCTTCTTAGAGGGACGGGCGGCGTTTAGCCGCACGAGATTGAGCAATAA
Hk  AGACGTTGGATCCCTT-GTGGGTCCAACGCAGCTTCTTAGAGGGACGGGCGGCGTTTAGCCGCACGAGAATGAGCAATAA
Tk  AGACGTCGGATCCCTTTGTGGGTTCGTCGCAGCTTCTTAGAGGGACGGGCGGCGTTTAGCCGCACGAGATTGAGCAATAA

Ck  CAGGTCTGTGATGCCCTTAGATGTTCTGGGCTGCACGCGCGCTACACTGAAGAAAT-CAGCGTGTGCTCCCTATCCGAAA
Hd  CAGGTCTGTGATGCCCTTAGATGTTCTGGGCTGCACGCGCGCTACACTGAAGAAAT-CGGCGTGTGTTCCCTATCCGAAA
Gr  CAGGTCTGTGATGCCCTTAGATGTTCTGGGCTGCACGCGCGCTACACTGAAGAAATGCAGCGTGTGTTCCTTATCCGAAA
Og  CAGGTCTGTGATGCCCTTAGATCTTCTGGGCTGCACGCGCGCTACACTGAAGAAAT-CAACATGTCTTCCCTATCCGAAA
Ic  CAGGTC-GTGATGCCCTTAGATGTTCTGGGCTGCACGCGCGCTACACTGAAGGAAT-CAGCGTGTGTTCCCTATTCGAAA
Hk  CAGGTCTGTGATGCCCTTAGATGTTCTGGGCTGCACGCGCGCTACACTGAAGGAAT-CAGCATGTGTTCCCTGTCCGAAA
Tk  CAGGTCTGTGATGCCCTTAGATGTTCTGGGCTGCACGCGCGCTACACTGAAGGAAT-CAGCGTGTGTTCCCTATTCGAAA
```

```
Ck  TTCTCTTTACTGAGTGCTTTGAGTGGCCAGCACGTTTACTTTGAAAAAATTGGAGTGCTCAAAGCAGGCGCTACAGCCTG
Hd  TTCTCTTAATCGAGTGCCTTGAGTGGCCAACACGTTTACTTTGAAAAAATTGGAGTGCTCAAAGCAGGCGCTACAGCCTG
Gr  TTCTCTTAACCGAGTGCCATAAGTGGCCAGCACGTTTACTTTGAAAAAATTGGAGTGCTCAAAGCAGGCGCTACAGCCTG
Og  TTGTCTTAACCGATTGCTATGAGTGGCCAGCACGTTTACTTTGAAAAAATTGGAGTGCTCAAAGCAGGCGCTACAGCCTG
Ic  TTCTCTTAATCGAGTGCCATAAGTGGCCAGCACGTTTACTTTGAAAAAATTGGAGTGCTCAAAGCAGGCGCTACAGCCTG
Hk  TGCTCTTAATCGGGTGCCTTGAGTGGCCAGCACGTTTACTTTGAAAAAATTGGAGTGCTCAAAGCAGGCGCTACAGCCTG
Tk  TGGTCTTAACCGATTGCTATATGTGGCCAGCACGTTTACTTTGAAAAAATTGGAGTGCTCAAAGCAGGCGCTACAGCCTG

Ck  AACATTAGTGCATGGAATAATAGAATAGGATCTCGGTTCTATTTTGTTGGCTTTCGGAGTCGAGGTAATGATTAATAGGG
Hd  AACATTAGTGCATGGAATAATGGAATAGGATCTCGGTTCTATTTCGTTGGCTTTCGGAGTCGAGGTAATGATTAATAGGG
Gr  AACATTAGTGCATGGAATAATGGAATAGGATCTCGATTCTATTTCGTTGGCTTTCGGAGTCGAGGTAATGATTAATAGGG
Og  AACATTAGTGCATGGAATAATGGAATAAGATCTCGATTTTATTTCGTTGGCTTTCGAAGTCGAGGTAATGATTAATAGGG
Ic  AACATTAGTGCATGGAATAATGGAATAGGATCTCGGTTCTATTTCGTTGGCTTTCGGAGTCGAGGTAATGATTAATAGGG
Hk  AACAATTGTGCATGGAATAATAGAATAGGATCTCGGTTCTATTTCGTTGGCTTTCGGAGTCGAGGTAATGATTAATAGGG
Tk  AACATTAGTGCATGGAATAATGGAATAGGATCTCGGTTCTATTTCGTTGGCTTTCGGAGTCGAGGTAATGATTAATAGGG

Ck  ACAGACGGGGGCATTCGTACTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGAACTACTGCGAAAGCATTTG
Hd  ACAGACGGGGGCATTCGTACTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGAACTACTGCGAAAGCATTTG
Gr  ACAGACGGGGGCATTCGTACTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGAACTACTGCGAAAGCATTTG
Og  ACAGACGGGGGCATTCGTACTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGAACTACTGCGAAAGCATTTG
Ic  ACAGACGGGGGCATTCGTACTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGAACTACTGCGAAAGCATTTG
Hk  ACAGACGGGGGCATTCGTACTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGAACTACTGCGAAAGCATTTG
Tk  ACAGACGGGGGCATTCGTACTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGAACTACTGCGAAAGCATTTG

Ck  CCAAGAATGTTTTCATTAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCATAAAC
Hd  CCAAGAATGTTTTCATTAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCATAAAC
Gr  CCAAGGATGTTTTCATTAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCATAAAC
Og  CCAAGAATGTTTTCATTAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCATAAAC
Ic  CCAAGAATGTTTTCATTAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCATAAAC
Hk  CCAAGAATGTTTTCATTAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCATAAAC
Tk  CCAAGAATGTTTTCATTAATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCCCTAGTTCTAACCATAAAC

Ck  GATGTCGACCAGCGATCCGTCGTCGTTAATTTTAATGACTCGACGGGCAGCTTCCGGGAAACCAGAGTGTTTGGATTCCA
Hd  GATGTCGACCGGCGATCCGTCGTCGTTAATATTAATGACTCGACGGGCAGCCTCCGGGAAACCAGAGTGTTTGGATTCCA
Gr  GATGTCGACCAGCGATCCGTCGTCGTTAAT-TGAATGACTCGACGGGCAGCTTCAGGGAAACCAAAGTGTTTGGATTCCA
Og  GATGTCGACCAGCGATCCGTAGTCGTTAA-ATGTATGACTCTACGGGCAGCTTCTGGGAAACCAAAGTTTTTGGATTCCA
Ic  GATGTCGACCGGCGATCCGTTGTCGTTAAC-TGAATGACTCAACGGGCAGCCTCCGGGAAACCAGAGTGTTTGGATTCCG
Hk  GATGTCGACTGGCGATCCGGCTCCGTTAAC-TGAATGACTAGCCGGGCAGTCTCTGGGAAACCAAAGTCTTTGGATTCAA
Tk  GATGTCGACCGGCGATCCGTCGTCGTTAAC-TGAATGACTCGACGGGCAGCCTCCGGGAAACCAGAGTGTTTGGGTCCCG
```

Ck GGATTGGA-AATCCGTTGAACCTTCTTCGTGATGGGGATTGGGGATTGCAATTATTCCCCATGAACGAGGAATT-CCAGT
Hd GGATTGGGAAGCCCGTTGAACCTTCTTCGTGATGGGGATTGGGGATTGCAATTATTCCCCATGAACGAGGAATTGCCAGT
Gr GGATTGGGCAACCCGTTGAACCTTCTTCGTGATGGGGATTGGAGATTGCAATTATTCTCCATGAACGAGGAATTCCCAGT
Og GGATTGGGTAATCCGTTGAAACTTCTTCGTGATGGGGATTGGAGATTGCAATTATTCTCCATGAACGAGGAATT-CCAGT
Ic GGATTGGGAAACCCGTTGAACCTCCTTCGTGATGGGGATTGGGGATTGCAATTATTCCCCATGAACGAGGAATTCCCAGT
Hk GGATCGGGAAACCCTCTGAACCTCCTTCGTGATGGGGATTGGCGATTGCAATTATTCCCCATGAACGAGGAATTCCTAGT
Tk GGATTGGGCAACCCGTTGAACCTCCTTCGTGATGGGGATTGGGGATTGCAATTATTCCCCATGAACGAGGAATTCCCAGT

Ck AGGCGCGAGTCATAAGCTTGCGTCGATTACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATCGAGTGATT
Hd AGGCGCGAGTCATAAGCTTGCGTCGATTACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATCGAGTGATT
Gr AGGCGCGAGTCATAAGCTTGCGTCGATTACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATCGAGTAATT
Og AGGTGCCAGTCATAAGCTTGCGCCGATTACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATCGAGTGATT
Ic AGGCGCGAGTCATAAGCTTGCGTCGATTACGTCCCTGCCCTTTGTACACACCGCCCGTGGCTACTACCGATCGAGTGATT
Hk AGGCGTGAGTCATCAGCTTGCGTCGATTACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATCGAGTGATT
Tk AGGCGCGAGTCATAAGCTTGCGTCGATTACGTCCCTGCCCTTTGTACACACCGCCCGTCGCTACTACCGATCGAGTGATT

Ck TAGTGAGGACTTCGGACTGGTCTTCGATGTGGCTTTACGGTCGTGTCGTTGTGCCGGAAAGATGCCCAAACTTGATTACT
Hd TAGTGAGGACTTCGGACTGGTCTTCGATGTGGCTTCCGGGTCGTGTCGGAGTACCGGAAAGATGCCCAAACTTGATTACT
Gr TAGTGAGGACTTCGGACTGGTCTTCGATGTGGCTTTCGGGTCGTGTCGGAGTTCTGGAAAGATGTCCAAACTTGATTATT
Og TAGTGAGGACTTCGGACTGGTCTTCGATGTGGCTTTCGGGTCGTGTCGGAGTGCCGGAAAGATGCCCAAACTTGATTACT
Ic TAGTGAGGCCTTCGGACTGGTCTTCGGTATGGCTTTCGGGTCGTGCCGGAGTACCGGAAAGATGACCAAACTTGATCACT
Hk TAGTGAGGCCTTTGGACTGGTCTTCGTTATGGCCTTCGGGTCGTGCCGGAGTACCGGGAAGATGACCAAACTTGATTACT
Tk TAGTGAGGACTTCGGACTGATCTTCAATGTGGCTTTCGGGTCATGCCGTAGTTTCGGAAAGATGCCCAAACTTGATCACT

Ck TAGAGGAAGTAAAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTA
Hd TAGAGGAAGTAAAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTA
Gr TAGAGGAAGTAAAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTA
Og TAGAGGAAGTAAAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTA
Ic TAGAGGAAGTAAAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTA
Hk TAGAGGAAGTAAAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTA
Tk TAGAGGAAGTAAAAGTCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTA

## REFERENCES


BÖRNER, C., 1901, Vorlaufige Mitteilung über einige neue Aphorurinen und zur Systematik der *Collembola*. Zool. Anz., **23**: 1-15.

CASSAGNAU, P., 1971, La phylogenie des Collemboles à la lumière des structures endocrines rétrocérébrales. 1. Sym. Intern. Zoolfilog., Univ. Salamanca, pp. 333-349.

CHRISTIANSEN, K., P., BELLINGER, 1980, The *Collembola* of North America. Grinnel College, **3**: 785-1027.

DALLAI, R., V., SBORDONI, M. C., SBORDONI, E., DE MATTHAEIS, 1983, Chromosome and enzyme diversity in some species of *Neanuridae* (*Collembola*). Pedobiologia, **25**: 301-311.

FANCIULLI, P. P., R., DALLAI, R. PETRUCCI, 1985, A preliminary study on enzyme diversity in *Tetrodontophora bielanensis* (WAGA)(*Insecta, Collembola*). Rev. Écol. Biol. Sol., **22(4)**: 483-495.

FANCIULLI, P. P., R., DALLAI, R., PETRUCCI, 1986a, Chromosomal and isozymic analysis in three populations of *Lathriopyga longiseta*. (In:) R. DALLAI (ed.), 2nd International Seminar on *Apterygota*, University of Siena: 203-210.

FANCIULLI, P. P., R., DALLAI, R., PETRUCCI, 1986b, Enzymatic polymorphism in geographically isolated populations of *Thaumanura ruffoi*. (In:) R. DALLAI (ed.), 2nd International Seminar on *Apterygota*, University of Siena: 197-202.

FANCIULLI, P. P., F., FRATI, R., DALLAI, J. RUSEK, 1991, High genetic divergence among populations of *Tetrodontophora bielanensis* (*Insecta, Collembola*) in Europe, Rev. Écol. Biol. Sol., **28(2)**: 165-173.

FELSENSTEIN, J., 1985, Confidence limits on the phylogenies; an approach using the bootstrap. Evolution, **39**: 783-791.

HIGGINS, D. G., A. J., BLEASBY, R. FUCHS, 1992, Clustal V: improved software for multiple sequence alignment, CABIOS, **8**: 189-191.

HWANG, U. W., B.-H., LEE, W., KIM, 1995, Sequences of the 18S rDNAs from two Collembolan insects: shorter sequences in the V4 and V7 regions, GENE, in press.

JUKES, T. H., C. R., CANTOR, 1969, Evolution of protein molecules in Mammalian Protein Metabolism (In:) H. N. MUNRO (ed.), Academic Press, NY, pp. 21-132.

KIM, W., L. G. ABELE, 1990, Molecular phylogeny of some decapod crustaceans based on 18S rRNA nucleotide sequences, J. Crustacean Biol., **10(1)**: 1-13.

KIM, W., G. S., MIN, S. H., KIM, 1992, The 18S rRNA gene of a crustacean decapod *Oedignathus inermis*: a comparison with *Artemia salina* gene, Nucleic Acids Res. **20**: 4658.

KUMAR, S., K., TAMURA, M., NEI. 1993, Molecular Evolutionary Genetics Analysis Ver. 1.01. Institute Molecular Evolutionary Genetics, Pennsylvania State Univ., Univ. Park, U.S.A.

LEE, B.-H., 1985. Cladistic analysis of *Neanuridae* (*Collembola*) using character weighted and character unweighted approaches, Korean J. Syst. Zool., **1**: 3-20.

LEE, B.-H., W. K., LEE, H. R. KIM, 1984, A Systematic Investigation of Korean *Tomoceridae* (*Collembola*), Kor. J. Entomol., **14**: 5-17.

LEE, B.-H., Y. J., KIM, H. Y. ,YANG, K.-H. PARK, 1985, A systematic investigation of Korean Entomobryidae (*Collembola*), Kor. J. Entomol., **15(2)**: 7-16

LEE, B.-H., J.-M., THIBAUD, 1987, A critical review of the taxonomy of *Gulgastrura reticulosa*, a cave *Collembola* from Korea, Syst. Entomol., London, **12**: 73-79.

LEE, B.-H., K.-H., PARK, 1991, A Systematic Study of Korean *Entomobryidae* (*Collembola, Insecta*) Based on Cladistic Analysis of Phenotypic and Allozyme Data, Kor. J. Zool., **34(2)**: 265-288.

MASSOUD, Z., 1976, Essai de synthese sur la phylogenie des Collemboles, Rev. Écol. Biol. Sol., **13**: 241-252.

MAYNARD, E. A., 1951, A monograph of the *Collembola* or springtail Insects of New York State, Comstock Publ. Comp., Inc. Cornell Univ. Ithaca, New York, pp. 339.

PACLT, J., 1956, Biologie der primär flügellosen Insekten. Jena, pp. 258.

PEARSON, W. R., 1990, Rapid and sensitive sequence comparison with FASTP and FASTA. (In:) R. F. DOOLITTLE (ed.), Molecular evolution: computer analysis of protein and nucleic acid sequences, Academic Press, pp. 1-736.

SAITOU, N., M. NEI, 1987, The neighbor-joining method: a new method for reconstructing phylogenic trees, Mol. Biol. Evol., **4**: 406-425.

SALMON, J. T., 1964, An index to the *Collembola*, vol. 1-11. Royal Soc. New. Zeal. , Wellington, Bull. 7: 1-144, 145-644.

SPEARS, T., L. G., ABELE, W. KIM, 1992, The monophyly of brachyuran crabs: A phylogenetic study based on 18S rRNA, Syst. Biol., **41**(**4**): 446-461.

SWOFFORD, D. L., 1990, Phylogenetic analysis using parsimony (PAUP), Version 3.0, Champaign: Illinois Natural History Survey (Computer program)

UCHIDA, H., 1971, Tentative key of the Japanese genera of *Collembola* in relation to the world genera of this order, 1. Sci. Rep. Hirosaki Univ., **18**: 64-76.

YOSII, R., 1961, Phylogenetische Bedeutung der Chaetotaxie bei den Collembolen, Cont. Biol. Lab. Kyoto Univ., 12: 1-37.